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Parent-offspring Invasion in Natural Populations of *Scilla scilloides*. 1. Effect of Recurrent Habitat Disturbance.

井原正昭* ツルボの自然集団に於ける世代置換。 1.繰返されるかく乱の影響。

Recent advances in population biology have visualized ecological as well as genetic uneveness of population structure in plant and animal species (e. g. KERSHAW 1958 ; SNAYDON 1962 ; ALLARD & JAIN 1962 ; LEWONTIN & HUBBY 1966). The uneveness is generally understood as the resultant of either interwoven effect of natural selection and breeding system or uneveness of selective forces due to patchy structure of the habitats.

However, the local population structure in plant species is evidently contributed by birth and death of its inhabitants as well as their emigration and immigration, which must bear any relation to the uneveness. Yet there is still limited accumulation of knowledge as to amphimictic recovery of offspring (ALLARD & JAIN 1962 ; ASTON & BRADSHAW 1967 and others) and inhabitant's life span (e. g. HARPER 1967) as well as pollen flow and seed dissemination (cf. LEVIN & KERSTER 1974).

Therefore, examination of parent-offspring invasion may be essential to the more balanced view of intra- and interpopulational dynamics in nature. In this connection the present series of study have been undertaken in *Scilla scilloides*, which inhabits more or less disturbed or man-made habitats.

Material and Methods

Thirty-eight flowering bulbs of *Scilla scilloides* (LINDL.) DRUCE were collected by Mr. Sigeru YAMAMORI from crop-fields along a foot-path toward Mt. Sekidouzan, Ishikawa-ken and sent to the writer on September, 1965. The outline map of the population site (Fig. 1) was re-drawn from informations provided by Mr. YAMAMORI. Cytological processing was undertaken in root-tip cells of respective bulbs by means of a modified TSUJIO and LEVAN' aceto-orcein-squash method as reported previously (SATOMI & IHARA 1963). Observation was made by a Nikon model S light microscope at the

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magnification of 150 to 1500, and thus their karyotypes of 25 clones were determined. Some critical preparations were photographed for karyograms and also sketched to aid convinient processing. In the present paper each karyotype is classified as in the previous one (IHARA 1966) and regarded as genotype for the reason mentioned elsewhere (IHARA 1977). Statistically to assess significance of localization pattern of the inhabitants under any hypothetical distribution, Chi-square statistics were calculated by the aid of a Casio electoric calculator Fx-19 and the figures of wanted probabilities were consulted with the Numerical Table of YOSHIDA and YOSHIDA (1958).

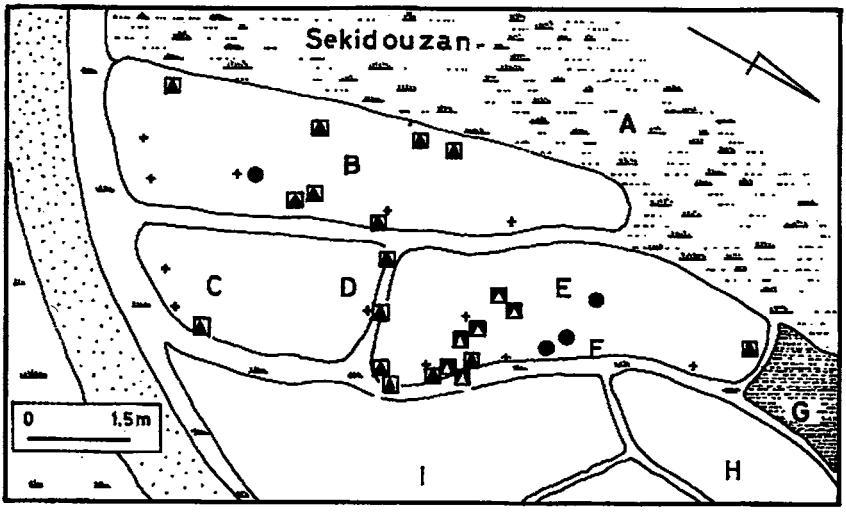

Fig. 1. Outline map of the population site of *Scilla scilloides* at Sekidouzan, Ishikawa-ken. Crosses represent the location of clones which were not examined in the present study. Solid circles, squares with solid triangle, and squares with open triangle indicate the positions of inhabitants of BB, ABBB and AB' BB, respectively. Keys to the habitat conditions are as follows : A & G (areas covered by *Phragmatis communis*), B & F (crop-fields of *Azukia angularis*), C (the cultivating area of *Brassica Rapa* var. *amplexicaulis*), D (*Raphanus sativus* var. *hortensis*), and H & I (rice-fields).

Results

Chromosomal characteristics in marker plants Out of 25 clones examined, 4 clones were diploid of BB, and 21 clones were allotetraploid of ABBB, in

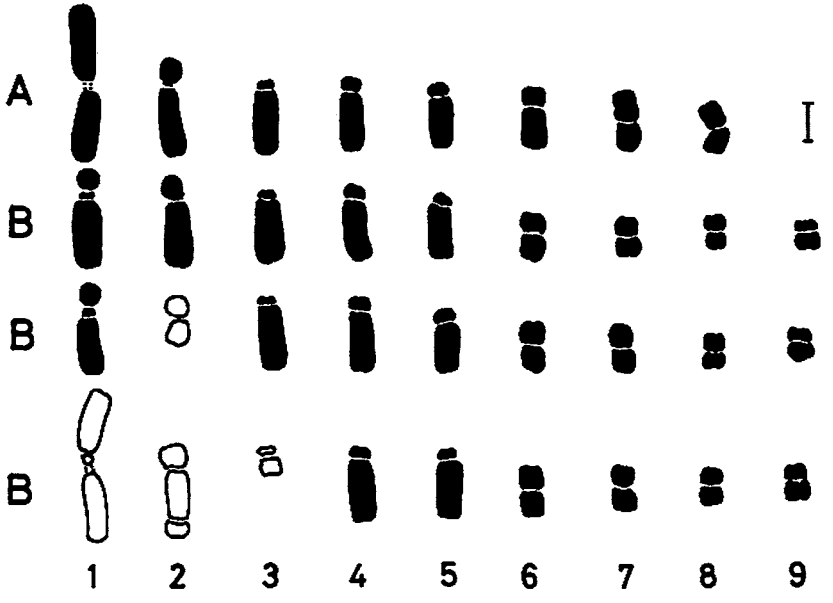

Fig. 2. Karyogram illustrating a modified allotetraploid of AB'BB which possesses 4 variants in the B complements. A marker locating at the top right corner represents 3.47 μm. All drawings were traced according to the original photomicrograph (IHARA 1966).

which 6 bulbs exhibited a modified form of the ABBB (Fig. 2 & Table 1). None of amphidiploid AABB was detected. As shown in the figure, the set may contain four modified chromosomes ; they are constituents of the B complements. A large median chromosome of the variants resembles to the A's marker chromosome (A_1) but the varriant possesses secondary constriction at the proximal end of the long arm. The second largest variant also reveals secondary constriction at the distal end of the long arm. The third one is a small chromosome with sub-median constriction, which is somewhat indiscernible from either one of A_8, B_6 or B_7. The fourth variant chromosome is a small one with terminal constriction which is very characteristic of the short arm of B_3.

An indirect demonstration may be possible to the origin of these variants : The largest varriant may have been resulted by translocating a part of the long arm of either normal B_2 or B_3 to the short arm of B_1. The translocation may be contributed by the long arm of B_2, so that

reasonable gain and loss were undergone in the chromosome arms of both B_1 and B_2. In consequence the B_2 resulted in the third varriant. There may be no reliable evidence for explaining the origin of the second largest chromosome. It is a possible explanation that the second and the fourth variants were resulted from B_2 and B_3 chromosome of the normal set by deletion of a part of the long arm of the B_3 with or without relation to the visualization of the secondary constriction in the B_2 variant.

In any case it would be sure that at least one translocation and one deletion participate for the origin of these four variants, which in turn suggests that initial causality of these two sequential events would be different from that of hyper- or hypo-aneuploid in ABBB (cf. IHARA 1966). Further, it is positively assumed that the mother bulb of all the variants would be descended by a single event and that they would have been propagated vegetatively. This is a basic assumption to follow their intrapopulational dispersion.

Spatial pattern of the inhabitants Location of respective genotypes is shown in Fig. 1, where their inhabiting pattern is seen as being somewhat localized. Amphimicts of the BB genotype explore their habitat by dissemination while almost obligate apomicts of the ABBB genotype would be restricted to their original location owing to low seed-yields. Accordingly, there may be any

Table 1. A 2 × 3 contengency table of nearest-neighbour's genotypes in the sample of *Scilla scilloides* at Sekidouzan, Ishikawa-Ken.

base genotype	nearest-neighbour's pairing		Σ
	homogeneous	heterogeneous	
BB	3 (0.50)	1 (3.50)	4 (4.00)
ABBB	11 (8.75)	4 (6.25)	15 (15.00)
AB'BB	5 (1.25)	1 (4.75)	6 (6.00)
Σ	19 (10.50)	6 (14.50)	25 (25.00)

(i) against homogeneous distribution

$X^2 = 0.2376$　df $= 2$　$p = 0.90-0.80$

(ii) against random assortment

$X^2 = 48.0831$　df $= 3$　$p < 0.001$

(the figures in parenthesis are those expected)

difference of inhabiting pattern between these two. Supposing that the sampling was unconciously made, a negligible bias would be expected as to the spatial pattern of the inhabitants. Further, these inhabitants would have been shuffled recurrently because of cropping. Localization pattern may be expressed as nearest-neighbour's heterogeneity in chromosome composition.

The first test is to assess homogeneous distribution among these genotypes ; otherwise the nearest-neighbours may form unique pairing in each chromosome constitution. In this regard, Chi-square statistics resulted as being $X^2 = 0.2376$, $df = 2$ and $p = 0.90 - 0.80$, which means that the spatial patterns of respective genotypes are similar, irrespective of their distributional patterns to be aggregative or divergent. More powerful analysis may be required for the detection of their distribution under random assortment. An expected value of homogeneous pairings of nearest-neighbour in the BB genotype is turned out to be $(3/24) \cdot 4$ and that of heterogeneous pairings is given as being $(21/24) \cdot 4$; likewise both cases of ABBB and AB^{t}BB would be calculated as shown in Table 1 (see the figures in parenthesis). Chi-squre statistics result in being $X^2 = 48.0831$, $df = 3$ and $p < 0.001$, which indicates that their inhabitation significantly deviates from random assortment. In other words, it is highly probable that they inhabit in aggregating. Alternatively, it may need to examine whether or not their spatial pattern can be expected by a sampling bias under equal frequency of homogeneous pairing (p_i) to heterogeneous pairing (p_j) in respective genotypes. A direct calculation of the probability is given as follows : $p = (19!\ 6!\ 4!\ 15!\ 6!) / (25!\ 3!\ 11!\ 4!\ 5!) = 1.849 \times 10^{-1}$. Thus, $p_i = p_j$ may result in $p_i > p_j$ by such a chance. That respective genotypes inhabit in aggregating is obvious.

If the above-mentioned conclusion is correct, the present spatial pattern would exemplify intrapopulational migration of bulbs or bulblets in *Scilla scilloides* because of extraordinary low seed-yields in ABBB (cf. IHARA 1966). Furthermore, the result may throw a question upon effect of dispersion in a short term. The fact that the variant forms of AB^{t}BB were inhabiting within the range of 2.0 meters, even though recurrent shuffling would have been occurred by ploughing, is a strong demonstration of extremely limited migration. Nevertheless, it is noteworthy that the chromosomal constitution of the present population is definitely common to those of the hill-side populations at the Namerikawa region in Toyama, where 31 natural populations were examined (IHARA 1977). These evidences imply that human activities have been less effective to intra- and interpopulational migration of *Scilla*

scilloides in a short term than what has been suspected in inhabitants of man-made habitats (see MAEKAWA 1942).

Discussion

The present cytological findings may be concerned with the origin of the variants from the evolutionary points of view. The assumption of all of their amphimictic recovery would meet with more difficulty than that in their apomictic origin : Such a chance would be extraordinary rare because of rare chance of subsequent two events in the chromosomal mutation to occur in the meiotic process, of low seed-yields in the ABBB plants and of considerably rare survival from the amphimictic newborns to the adults. Furthermore, all of these variants were synchronously bearing flowers, so that they would have survived for more than several years because it takes at least three years from seedling stage to the flowering stage in amphidiploid of AABB which is the most rapid growing genotype in the species (IHARA unpublished). These evidences reinforce that the marker plants with AB^{1}BB have descended from a common origin by vegetative propagation.

Provided that the above-mentioned assumption is admitted, we would expect that the normal allotetraploid propagates by the same rate as AB^{1}BB does, indicating that vegetative propagation prevails over amphimictic one in this population. In fact, allotetraploid plants of almost obligate apomicts remarkably exceed diploid plants of amphimicts with habitual apomixis in the population, even if any sampling bias is involved in the information (Table 1). Thus, it is assumed that vegetative propagation has a positive effect on the life span of the plants because the variants would have been maintained without any amphimictic recovery after they descended from a common origin. Therefore, it would be concluded that habitat disturbance results in prolongation of their life span of obligate or habitual apomicts, in which the more recurrent disturbance the longer the life span may be a rule to some extent. Further, the prolongation of the life span by habitat disturbance would compensate disadvantage of a parent-offspring substitution in obligate or habitual apomicts in view of the maintenance of the population.

If this is a general rule, a question would arise : Does recurrent disturbance play any role in maintaining chromosomal or genetic polymorphism whatever its origin may be ? Since recurrent disturbance is suspected to effect advantageously on vegetative as well as amphimictic propagation (IHARA 1977), maintenance of the polymorphism may be due to neither recombination of patchy structures in the habitat nor ordinary selective modification of inhab-

itant's frequency but due to the prolongation of the life span itself. It is self-evident that the prolongation would be followed by prevention of homogeneizing constituent's age constitution, which in turn results in coexistence of genetically heterogeneous inhabitants if they are neutral to the habitat disturbance. Probably it is a supporting evidence that European and Asian "viviparous alliums" (e. g. *Allium vineal*, *A. grayi* and others) exhibit chromosomal polymorphism (IHARA unpublished ; KURITA & KUROKI 1964).

Alternative explanation is possible for maintenance of heterogeneous constituents in the disturbed habitats : Multiple niche or patchy work of the habitat must be easily attained by ploughing and bedding for crops, so that the species here under consideration would arrive at its preferable inhabiting sites and would found new colonies at respective sites (cf. LEVENE 1953 ; CHRISTIANSEN 1974 ; LEVIN & PAINE 1974). However, this seems to be unlikely because only insufficient number of inhabitants may participate in the exploration. Further accumulation of data is essential to assess the present proposal (also see IHARA 1977). The writer expresses his cordinal appreciation to Mr. Shigeru YAMAMORI for his collecting the present materials.

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摘　　要

石川県鹿島郡石動山の登山道沿いの畑からツルボの開花個体を38株サンプルして貰い，そのうち25株の核型を調査したところ，4株はBB(2n＝18)，15株はABBB(2n＝35)及び6株はAB^{t}BB (Fig. 1) であった。AB^{t}BBには4個の変形した染色体が含まれ，それらの起源には少くとも1個の転座と1個の欠失が関与したものと想定される。この様な染色体突然変異が起る確率は通常極めて低く，更にABBBに於ける種子生産が低いことを考え合わせると，この集団でこの変異株がこの様な割合で生存するのはただ一回の事象で産出された親変異株から無性的に繁殖したことによるものと推論される。この推論に立脚して，くり返し生育地のかく乱が行われる場合の集団内移住及び集団構造の変化について，かく乱による個体の延命と言う観点から考察が行われた。